# The Spatial Pattern of Invading Pinus radiata

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The spatial pattern of invading populations can provide insight into mechanisms of invasion and help establish the potential for further spread of a species. *Pinus radiata* has successfully invaded native vegetation across southeastern Australia. The small scale spatial pattern of invading *Pinus radiata* was investigated within two dry Eucalypt woodlands adjacent to commercial plantations in the upper Blue Mountains, NSW Australia. This study aimed to identify the presence of a second generation of pines in order to determine the sustainability of the invading population. We looked for evidence of 1) clustering of pine seedlings; 2) positive associations between pine seedlings and reproductive pines. Spatial analysis of 20 m by 20 m plots using dispersion indices and Ripley's K function revealed clustering of pine seedlings at distances of up to 450 m from the plantation. Bivariate analysis found significant positive association between seedlings and reproductive pines in two plots. Further evidence for self propagation was provided by the correlation between seedling abundance and cone abundance. These results suggest that the invading population is sustainable in the long term and is capable of spreading further into the native vegetation.

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#### INTRODUCTION

The tree *Pinus radiata* has successfully spread from commercial plantations into adjacent natural areas across the southern hemisphere where it is widely planted as a commercial timber crop (Richardson et al. 1994). Pine invasions are of particular concern in New Zealand and South Africa where they are threatening ecological and aesthetic values (Richardson et al. 1994, Ledgard 2001). Dense stands of self sown pines can suppress understorey vegetation (Richardson and Van Wilgen 1986, Richardson et al. 1989), and alter a range of ecosystem properties including hydrology (Van Wyk 1987), nutrient cycling and fire regimes (Versfeld and Van Wilgen 1986).

The first phase of invasion by pines involves the dispersal of seed, typically by wind, from plantation trees and the subsequent establishment of wildlings in the recipient habitat. The cones of *Pinus radiata* are serotinous, opening and releasing seed during hot, dry weather conditions and after fire (Fielding 1947, McDonald and Laacke 2003). While the majority of seeds are dispersed less than 100m from parent trees (Van der Sommen 1978 cited in , Virtue and Melland

2003), initial recruits can establish at long distances of up to 4km from the plantation (Williams and Wardle 2005) and have been referred to as satellite foci (Richardson et al. 1994). Yellow-tailed black cockatoos (*Calyptorhynchus funereus*) may also be responsible for long distance dispersal events as they feed on cones and carry away seed (Attiwill 1970, Buchanan 1989, Gill and Williams 1996). Rare long distance dispersal events leads to a broken invasion front and patchy progress across the landscape (Hengeveld 1989).

The second phase of invasion occurs when first generation wildlings mature and begin to reproduce, creating a secondary seed source. Pines are known to self-fertilise and perpetuate by establishing a colony of seedlings (Bannister 1965). Self reproduction from new loci located beyond the main invasion front contributes greatly to the invading population (Moody and Mack 1988) and increases invasive spread rates (Clark et al. 1998). Seed dispersal processes are central components of invasion dynamics and are integral to models of pine spread which hope to gain a predictive understanding of invasions (Higgins and Richardson 1998). Determining the presence of a second generation of invaders and establishing the time to their successful establishment will assist the parametisation of models and the estimation of pine spread rates.

Detecting the occurrence of pine wildling reproduction requires an ability to distinguish between seedlings sourced from the plantation and those recruited from first generation colonisers. The spatial relationship between adult and juvenile plants can provide insight into dispersal patterns and seedling origin. Limited seed dispersal can lead to small scale aggregation of individuals (Prentice and Werger 1985). Positive associations between seedlings and parent plants have been attributed to seed dispersal mechanisms in a savanna palm tree population (Barot et al. 1999). Similarly, the dispersal of seed by pine wildlings would result in the aggregation of seedlings and a positive association between these seedlings and reproductive adults. Post-germination processes and conditions including environmental heterogeneity (Manabe and Yamamoto 1997), herbivore activity (Janzen 1970) and competition with the mother plant (Augspurger 1984) will influence seedling survival and may result in a seedling distribution which disguises the initial clustering of seeds around the parent plant. Therefore, the detection of a clustered spatial pattern after these processes have influenced seedling distribution provides evidence for the natural regeneration of pines.

Continuous dispersal of seed from the plantation itself may also disguise natural regeneration patterns. Seed in areas near to the plantation will arrive from two sources; the plantation and first generation wildlings. Constant seed dispersal from plantation trees will result in a random pattern of seedlings in the native vegetation, whereas recruitment from already established wildlings will lead to a clustering of seeds around reproductive adults. In areas where first generation wildlings are the primary seed source, i.e at distances away from the plantation, you would expect to find a more detectable clustering pattern.

Invasions of *P. radiata* have been reported across southeastern Australia (Burdon and Chilvers 1977, Minko and Aeberli 1986, Lindenmayer and McCarthy 2001, Williams and Wardle 2005), however quantitative studies detailing the spatial pattern of the invader are scarce. Evidence for self generation of pines has been recorded within an invaded eucalypt forest in the Australian Capital Territory (Chilvers and Burdon 1983) where young seedlings were found to be clustered around pines with mature cones. The Blue Mountains region of New South Wales is particularly at risk of invasion by *P. radiata* with many plantations bordering large tracts of continuous native vegetation. Two areas in particular, Newnes and Lidsdale State Forests have suffered high levels of invasion with pine densities exceeding 1,000 per hectare in areas adjacent to the plantation (Williams and Wardle 2005). Observations of high numbers of pine seedlings clustered around reproductive adults at both sites suggested the presence of self propagation by wildling trees. This study aims to confirm the occurrence of wildling reproduction by investigating the small scale spatial pattern of invading *Pinus radiata* within the two Eucalypt woodlands. It was expected that spatial analysis of the survey area would identify clustering of pine seedlings and a positive association between pine seedlings and reproductive pines.

## METHODS

### **Study Sites**

The study took place in two state forests situated in the upper Blue Mountains in the central tablelands of New South Wales. Newnes State Forest (150°12'E, 33°24'S; altitude 1000-1170m) is located approximately 7.5 km north east of Lithgow, NSW and encompasses a 51 year old, 2000 hectare *P. radiata* plantation. Lidsdale State Forest (150°3'E, 33°26'S; altitude 900-1000 m) is situated approximately 7 km north west of Lithgow and includes a 46 year old, 580 hectare *P. radiata* plantation. Field work took place in February to August, 2003 within native vegetation adjacent to the pine plantations.

# **Field Sampling**

At each site, pine occurrence was investigated within 20 m by 20 m plots located along six transects placed perpendicular to the plantation boundary. Transects were placed on multiple borders of the plantation and ended when pines were no longer present or terrain prevented further investigation. Transects ranged in length from 150 m to 2.2 km at Newnes and from 200 m to 750 m at Lidsdale. Plots were placed in the nearest vegetation to the plantation edge avoiding any forestry roads or fire breaks and were established at regular intervals within each transect. The distance between plots varied from 100 m to 200 m to reflect changes in pine density. In total 28 plots at Newnes and 23 plots at Lidsdale were sampled.

Six of the plots at each site in the area of Eucalypt forest closest to the plantation were mapped. Mapped plots were established in the first available vegetation next to the plantation and located 50 m apart. Within these plots the position of all dead and living *P. radiata*  individuals was recorded in Cartesian coordinates to the nearest 0.1 m. For every pine inside the plot the position of the center of the tree (x and y coordinates) was recorded, the diameter at breast height, 1.4m (Dbh) was measured with a tape, the height estimated to the nearest 0.5 m and the number of cones and branch whorls were counted. A whorl is the cluster of branches arising from a node on the stem (Bannister 1962). Non mapped plots were divided into 16, five metre by five metre quadrats. Within each quadrat, the number of cones of *P. radiata* individuals with whorls was estimated and the Dbh recorded. *Pinus radiata* individuals without whorls were counted.

*Pinus radiata* individuals within all plots were divided into five categories. 1) Seedlings; no whorls present, 2) Saplings; whorls present and less than 1m in height, 3) Juveniles; Greater than 1m in height and a Dbh of less than 10cm, 4) Adults; trees with Dbhs of 10cm or more; 5) Reproductive; trees of any size with cones present.

#### **Spatial Analysis**

**Dispersion Indices** 

Non mapped data were analysed using the index of dispersion (ID) which estimates how a pattern departs from spatial randomness. The index is calculated as the ratio of mean to sample variance:

$$D = \sum_{i=1}^{n} \left( \overline{x}_i - x \right)^2 / \overline{x}$$

(Ludwig and Reynolds 1988)

A random arrangement of plants within the sixteen quadrats will have a frequency distribution similar to that of the Poisson distribution. Since the variance and mean are equal in Poisson distributions, a variance to mean ratio (ID) close to 1.0 is indicative of a random distribution (Dale 1999). Dispersion indices below 1.0 indicate a regular distribution while those greater than 1.0 suggest a clumped pattern.

Dispersion indices for pine seedlings were calculated for all plots with more than 10 seedlings present using the PASSAGE computer program (Rosenberg 2001). Juveniles and saplings were excluded from the analyses due to low numbers. Results were compared to  $\chi^2$  values to determine statistical significance at the p = 0.025 significance level.

## **<u>Ripley's K function</u>**

The use of dispersion indices to identify spatial pattern is limited as it produces a single index of non

randomness and fails to detect the scale at which this pattern occurs. Ripley's K function (Ripley 1977) considers the variance in nearest-neighbour distances (Haase 1995) and is favoured for its ability to detect pattern across a range of spatial scales. A circle of radius t is centred on each point and the number of neighbours within the circle is counted. Density  $(\lambda)$  is estimated by dividing the number of individual points present by the area sampled (A) ( $\lambda = n/A$ ). Ripley's K function, K(t), is defined as the expected number of points within distance t of a point, as a proportion of this estimated value for density. Under the null hypothesis of Complete Spatial Randomness (CSR)  $K(t) = \pi t^2$ . That is, the area of a circle of radius t and a plot of  $\sqrt{K(t)}$  versus t should be linear. An estimator of K(t) is calculated separately for every t (Appendix 1).

The distribution of pine seedlings within the twelve mapped plots was investigated with Ripley's K function using the SPPA computer program (Haase 2002). The analysis began at a radius t of 0 m with small 0.1 m increments up to 10 m (one half of the plot length) to investigate small scale patterns. The sample statistic was plotted as the derived variable L(t),

$$L(t) = \sqrt{\left(\frac{K(t)}{p}\right)} - t = 0$$
  
(Haase 2001)

as it has zero expectation for any value of t when the pattern is random (Skarpe 1991). This analysis was only performed for plots with 10 individuals or more, as a lower number will not reveal consistent patterns in the spatial distribution (Arevalo and Fernandez-Palacios 2003).

Monte Carlo simulations produced 99% confidence intervals. Positive values of L(t) above the upper limit of the confidence interval signified clumping at this scale. Significant negative deviation specifies a regular pattern (Diggle 1983), while L(t) values that remain within the confidence intervals support the null hypothesis of Complete Spatial Randomness (CSR).

### **Bivariate analysis**

Bivariate analysis is an extension of Ripley's K function and allows an investigation of the nature of a relationship between two different life stages of a species (Couteron and Kokou 1997). Alternatives to random bivariate patterns are clumped distributions suggesting positive association or regular patterns which suggest repulsion between two life stages.

The spatial relationship of two life stages, which

may have different densities,  $\lambda_1 = n_1/A$  and  $\lambda_2 = n_2/A$ is examined. The function  $\lambda_1 K_{12}(t)$  is defined as the expected number of individuals of species two within a radius t of an arbitrary individual of species one. The function  $\lambda_2 K_{21}(t)$  gives the expectation for the opposite spatial relationship. The corresponding estimators are then combined to a weighted mean single estimator (Lotwick and Silverman 1982) (Appendix 2). The derived K-statistic:

$$L_{12}(t) = \sqrt{[n_2 k_{12}(t) = n_1 K_{21}(t)]} / [(p (n_1 = n_2)] - t]$$

(Kenkel 1994, Haase 2001)

is then plotted for values of t. If the two species are independent of one another the expected value of  $L_{12}(t)$  is 0. Negative values of  $L_{12}(t)$  indicate a negative association while values of  $L_{12}(t)$  greater than 0 suggest that the pattern is attractive (Mouer 1993) at that distance.

To determine the relationship between pine seedlings and reproductive adults, bivariate analysis was performed for all mapped plots using the SPPA computer program (Haase 2002). Analysis of non mapped data

The ability to detect spatial association between reproductive adults and seedlings within non mapped plots is restricted by the low resolution of the quadrat data. This relationship was investigated on a slightly larger scale by considering the correlation between the number of cones on reproductive trees and the number of seedlings in a plot. A square root transformation of cone data was performed prior to calculation of correlation coefficients in order to account for the large variation in cone presence. Plots located adjacent to the plantation boundary were excluded from these calculations as it was assumed that seedlings in these plots are more likely to have been sourced from the plantation rather than the reproductive trees present.

#### RESULTS

#### **Distribution of seedlings**

Establishment of seedlings was not equal between plots with less than 10 seedlings counted in more than half of the plots surveyed indicating low levels of invasion in these areas. Eleven of the 28 plots at

Table 1. Clustering in *P. radiata* seedlings. Sample size (n), Index of dispersion (ID) and significance level for seedlings at Newnes and Lidsdale. Asterices (\*) indicate plots with significantly (p<0.025) clustered seedlings.

	NEWNES					LIDSDALE					
Plot	Distance from plantation (m)	n	ID	p – value	Plot	Distance from plantation (m)	N	ID	p - value		
IB	50	65	3.27	0.0000*	1B	50	13	1.84	0.0241*		
1C	50	86	2.80	0.0000*	1C	50	14	1.41	0.1299		
2D	50	25	0.83	0.7179	1E	50	77	4.27	0.0000*		
2E	50	50	6.08	0.0000*	5A	50	15	0.92	0.5407		
2F	50	11	1.15	0.0341	2A	150	13	0.86	0.6142		
3A	50	13	1.68	0.0479	4A	150	37	3.33	0.0380*		
4A	50	16	1.73	0.0380	5B	250	22	1.83	0.0252		
1D	150	30	6.18	0.0000*	4B	350	20	1.33	0.1719		
1E	250	12	12.00	0.0000*	2C	550	12	1.16	0.2993		
1F	350	60	4.53	0.0000*							
1G	450	16	2.67	0.0005*							

Newnes and 9 of the 23 plots surveyed at Lidsdale had more than 10 seedlings present and were analysed to determine the level of clustering. Dispersion indices for seedling distributions were greater than 1.0 in ten of the eleven plots at Newnes and in seven of the nine plots at Lidsdale, indicating tendencies towards clumping (Table 1). At Newnes, seven plots displayed significant results with IDs ranging from 2.67 to 12.0. Clustering was significant in three plots at Lidsdale. All plots at both sites with more than 25 seedlings were significantly clustered. There was some evidence for a greater degree of clustering in plots further from the plantation at Newnes with all four plots located more than 50m away returning significantly clustered results (Table 1). However, clumping was also present in plots close to the plantation and many plots were excluded from analysis due to low seedling numbers preventing a thorough examination on the effect of distance.

Analysis of the twelve mapped plots using Ripley's K function revealed significant clustering of seedlings across scales from 1 m to 9 m. All plots at both sites with greater than 25 seedlings present contained significantly clustered distributions (Fig. 1).

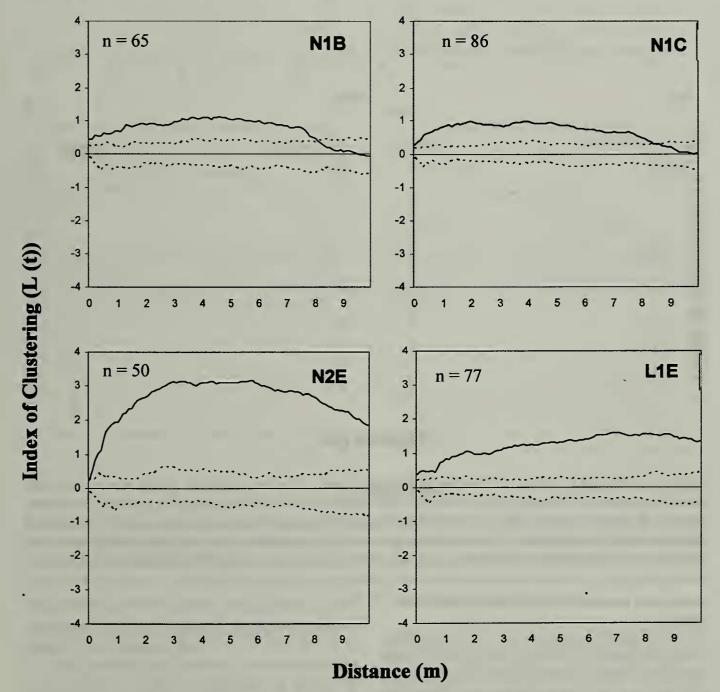


Figure 1. Spatial analysis of the distribution of all *P. radiata* seedlings for significantly clustered mapped plots at Newnes (N1B, N1C, N2E) and Lidsdale (L1E). L(t) values > 0 indicate clustering. The dotted lines give the 99% confidence intervals. Sample size (n) is in the top left corner and plot label is in the top right corner of each graph.

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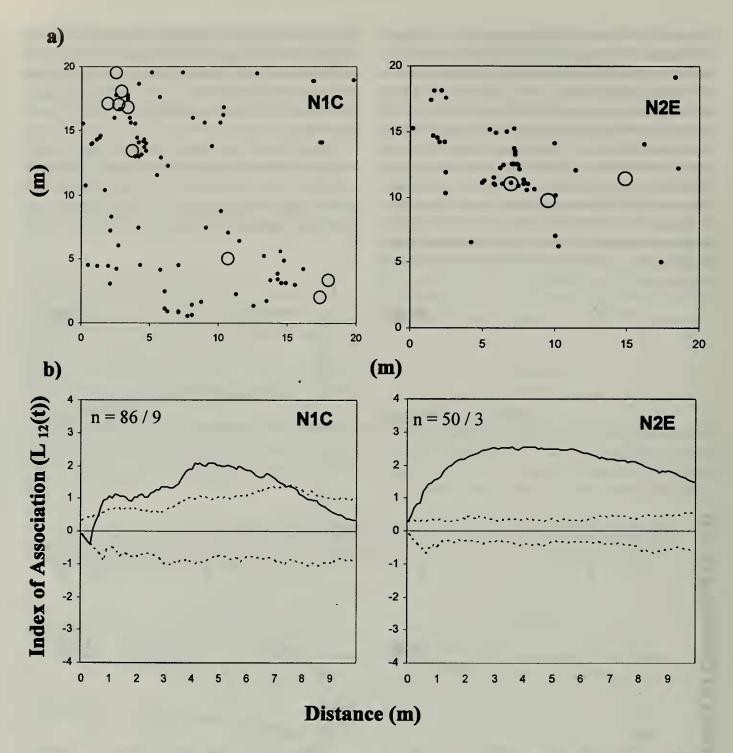
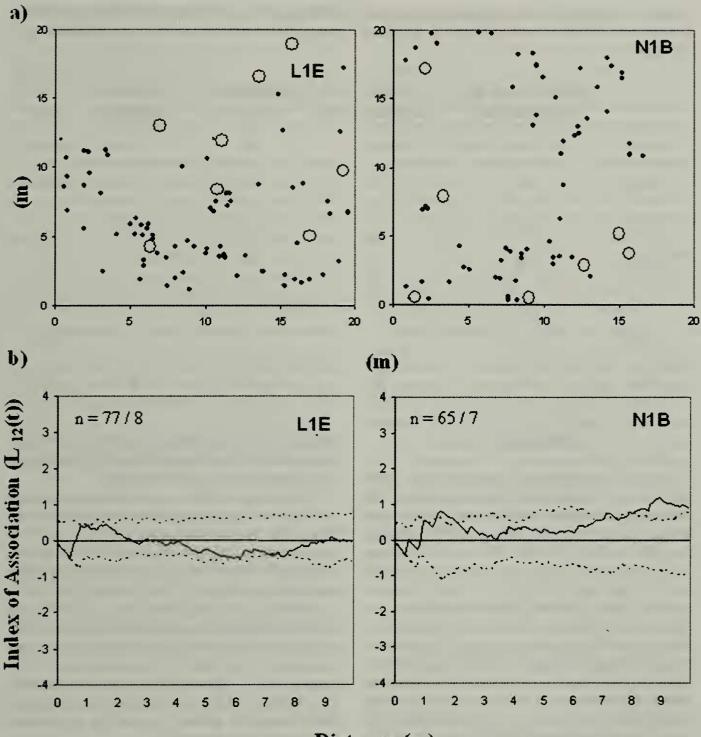


Figure 2 a) Mapped locations of *P. radiata* individuals within 20 m by 20 m plots. Large open circles represent reproductive *P. radiata*. Small closed circles represent P. radiata seedlings. b) Positive association between *P. radiata* seedlings and reproductive trees in two mapped plots at Newnes. L12(t) values > 0 indicate a positive association. The dotted lines give the 99 % confidence intervals. Plot label is in the top right corner and sample size (n) is in the top left corner of each graph: seedlings/reproductive trees.

# Association between seedlings and reproductive adults

When seedling number was low, no significant association between life stages was found at either Newnes or Lidsdale. Of the twelve mapped plots, only four had more than 25 seedlings present, two of which revealed significant positive associations. Maps indicating the position of *P. radiata* individuals in the plots illustrate the clustering of seedlings around reproductive adults (Fig. 2a). Bivariate analysis revealed a significant positive association at scales of 0.5 m to 7.5 m in plot 1C at Newnes and at all distances in plot 2E at Newnes (Fig. 2b). Seedlings were scattered across the remaining two plots (Fig. 3a). Bivariate analysis confirmed spatial independence between seedlings and reproductive trees despite high seedling abundance (Fig. 3b).



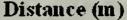


Figure 3. a) Mapped locations of *P. radiata* individuals within 20 m by 20 m plots. Large open circles represent reproductive *P. radiata*. Small closed circles represent P. radiata seedlings. b) Spatial relationship between *P. radiata* seedlings and reproductive trees in mapped plots at Lidsdale (L1E) and Newnes (N1B). L12(t) values > 0 indicate a positive association. The dotted lines give the 99 % confidence intervals. Sample size (n) is in the top left corner of each plot: seedlings/reproductive trees.

# Association between seedlings and reproductive adults in non mapped plots

Cone abundance per 20 m by 20 m plot was extremely variable ranging from 0 to 131 at Lidsdale and from 0 to 700 at Newnes. Significant positive correlations were found between square root cone abundance and seedling abundance for far plots at both sites (Lidsdale: r = 0.77, p < 0.001. Newnes: r = 0.76, p < 0.01). This relationship was most noticeable at Newnes where very large numbers of cones in transect one produced large numbers of highly clustered seedlings (Table 2). Plots within transect one had an average of 615 ( $\pm$  13.96) cones and 29.5 ( $\pm$  2.72) seedlings per plot. In comparison transect two contained only three cones in total and yielded no seedlings.

Plot	Distance from the plantation (m)	Number of reproductive trees	Total number of cones	Number of seedlings	ID
NID	150	35	685	30	6.2
N1E	250	4	700	12	12.0
N1F	350	6	620	60	4.5
NIG	450	4	456	16	2.7
N2G	150	0	0	0	NA
N2H	250	1	3	0	NA
N2I	350	0	0	0	NA

Table 2. Relationship between cone production and seedling presence and dispersion within transects 1 (Plots 1D, 1E, 1F, 1G) and 2 (Plots 2G, 2H, 2I) at Newnes. Plots placed adjacent to the plantation are excluded.

#### DISCUSSION

Many processes will influence the spatial distribution of seedlings within a population. These include seed dispersal mechanisms (Prentice and Werger 1985, Hatton 1989, Barot et al. 1999), distance from the mother plant and other seedlings (Janzen 1970, Augspurger 1984) and microsite conditions such as light availability (Arevalo and Fernandez-Palacios 2003) that will affect establishment. As many of these processes will produce similar patterns, care is needed in inferring causation. The process of prime interest in this study was that of seed dispersal. Generally, the result of initial seed dispersal is a clustered distribution of seeds around the mother plant (Bigwood and Inouye 1988). Recruitment from parent plants has resulted in aggregation patterns in a number of wind dispersed species (Westelaken and Maun 1985, Hatton 1989). While the seeds of P. radiata are adapted for long distance dispersal (Van Wilgen and Siegfried 1986), experimental data from the study sites indicates that the majority of seeds released from pine wildlings in the Eucalypt habitat will fall within 10 m of the parent tree with only rare long distance dispersal events witnessed. This pattern of seed dispersal leads to a clustering of seedlings around the parent plant detectable by the methods used in this study. Dispersion indices revealed tendencies towards clumping among seedlings within most plots. A general trend of greater clustering with increased sample size was found. This relationship

suggests that once seedling abundance is sufficiently high, a significant spatial pattern can be detected, and a clustered pattern is usually observed.

Significant positive associations between seedlings and reproductive trees were found in two plots at Newnes providing some evidence for natural regeneration within areas adjacent to the plantation. The spatial relationship between seedlings and adults may change with time. Higher survival and growth of seedlings close to the parent tree, 5-20 years after fire, can strengthen the aggregation pattern (Ne'eman et al. 1992). Spatial independence between seedlings and reproductive trees in two plots adjacent to the plantation with high seedling numbers also suggests that seedlings have originated from the plantation which therefore appears to provide an ongoing contribution to recruitment.

Other process unrelated to regeneration may also produce a pattern of clustered seedlings. Yellowtailed black Cockatoos, *Calyptorhynchus funereus*, have been known to feed on cones and carry them away (Buchanan 1989, Gill and Williams 1996) and were observed feeding on plantation trees at both study sites. The dropping of an entire pine cone by these birds may result in an aggregation of seedlings in the native vegetation, This event could occur at any distance from the plantation and separating this process from natural regeneration from wildlings is difficult. Genetic analysis of the wilding population is possible as microsatellite markers have already been developed for the species (Devey et al. 2002). However, while this may help confirm the patterns observed in this study it would fail to distinguish between wind and bird dispersed recruits. Determining the relative contribution of the two vectors to overall seed dispersal would be useful for modelling spread patterns as long distance dispersal events have been shown to be important for determining invasive spread rates (Buckley et al 2005).

Stronger evidence for the production of a second cohort of wildlings was provided by the relationship between the number of cones within a plot and the number of seedlings present. Seedlings were numerous and highly clustered in plots containing highly reproductive trees, suggesting that self regeneration of pines is occurring at distances of at least 450 m from the plantation. This observed pattern concurs with another study which recorded the establishment of seedlings around initial colonizers in an invasion of Pinus radiata into South African fynbos vegetation (Richardson and Brown 1986). The authors recorded high pine densities of more than 2,700 individuals per ha at distances of greater than one kilometre from the plantation. Investigation of the invading population found that initial colonisation occurred 13 years after plantation establishment and that sufficient seed was being produced by these recruits to generate a second cohort of invaders within only 21 years of afforestation. While first plantings of

*P. radiata* occurred 46 years ago at Lidsdale and 51 years ago at Newnes, the majority of planting took place between the years of 1973 and 1981 at both sites. *Pinus radiata* cone production peaks between about 10 and 20 years of age (Lewis and Ferguson 1993) which means that a considerable amount of seed has been available for over 20 years. The presence of a second generation of wildlings at Newnes and Lidsdale after this amount of time is not unexpected considering the timescale of invasion observed by Richardson and Brown (1986). We observed the establishment of new seed sources at distances of up to 450m from the plantation which may lead to further spread of the population into the native vegetation.

Seed production within the plantation itself has been shown to be a large determining factor in the pattern of recruitment in areas surrounding plantations (Dawson et al 1979). Peaks in the recruitment of first generation wildlings may result in a wave of second generation recruitment once wildlings enter peak cone production. Current knowledge of cone production within wildling populations is scarce and may assist with the management of invasions by establishing a time frame for the establishment of second generation pine invaders.

While results of this study suggest that first

generation wildlings are producing a second cohort of pines, the capacity of these individuals to contribute to the invading population and advance the invasion front will depend on their capacity to survive in their new environment. Environmental variation including suitable conditions for seedling establishment and survival will influence the rate of invasion (Richardson and Bond 1991). Preliminary investigations of seedling survival at Newnes suggest that establishment rates and short term survival are high following fire. However, this study also found that the majority of plots had very low numbers of seedlings indicating that while the pines have reached the second stage of invasion, the establishment process is slow. Further quantification of seedling survival rates is required to determine the long term sustainability of the invading pine population.

When inferring processes from pattern, it is essential to look at temporal changes of spatial distributions. Continued processes of recruitment and seedling mortality will change the spatial pattern of the invading pines. Monitoring of the pine population within the study area over a longer time period is desirable and may provide further evidence for the generation of a second cohort of wildlings. More importantly, the quantification of germination success and survival rates of pines in the native eucalypt vegetation will help determine spread rates and evaluate the significance of pines as an invasive species.

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# Appendix 1

Unbiased estimator of K(t):

$$\hat{K}(t) = n^{-2} A \sum_{I \neq j} w_{j}^{-1} I_{t}(U_{j})$$

(Ripley 1976, 1981)

A – area of the plot in m<sup>2</sup>  $I_i$  - counter variable  $U_{ij}$  – distance between events *i* and *j*  $w_{ij}$  – weighting factor to correct for edge effects

# Appendix 2

Estimators for bivariate analysis:

$$\hat{K}_{\mathbb{P}}(t) = (n_1 n_2)^{-1} A \sum \sum w_j^{-1} I_t(u_j)$$

(Lotwick and Silverman 1982)

$$\hat{K}_{2}(t) = (n_{2}n_{1})^{-1}A\sum_{i} \sum w_{j}^{-1}I_{t}(u_{j})$$

Combined estimator:

 $(n_1 + n_2) - 1 [n_2 K_1 (t) + n_1 K_1 (t]]$